PhD THESIS

Spontaneous regeneration and ecological restoration of degraded vegetation on sand

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INTRODUCTION AND OBJECTIVES

Land use change is one of the key drivers of biodiversity loss globally (Sala et al. 2000). Following change in land use, spontaneous regeneration of degraded ecosystems depends on ecosystem characteristics and land use history. Abiotic factors, local biotic interactions and propagule availability determine regeneration potential in parallel during secondary succession (Palmer et al. 1997). In case of low regeneration capacity, regeneration cannot take place within reasonable time frame and active ecological restoration is needed.

Pannonian sand grasslands in the Danube-Tisza Interfluve are endemic to the Pannonian biogeographic region. These grasslands form the grassland component of the Pannonian forest steppe (Molnár 2003). The spatial extent of the sand grasslands decreased significantly during the 19-20th centuries (Biró et al. 2008). 92 % of the open sand grasslands and 99 % of the closed sand grasslands were destroyed and converted mostly to agricultural fields and plantations until the end of the 20th century (Biró et al. 2011). Beside the changing spatial extent, the ecological condition of the sand grasslands is also altered due to degradation. Especially closed sand grasslands are degraded because of the regional lowering of soil water table (Molnár et al. 2008). Sand grasslands are also heavily affected by plant invasion. According to the national MÉTA survey (Actual Landscape Ecological Habitat Database), 70 % of the open sand grasslands and 30 % of the dry and semidry grasslands were threatened by invasion between 2000-2004 (Botta-Dukát 2008). Black locust and common milkweed (*Asclepias syriaca*) were the most important plant invaders of open sand grasslands according to the survey (Botta-Dukát et al. 2008).

Parallel to land use intensification, the least productive agricultural areas have been abandoned since the 1980s (Molnár and Biró 2011). Historically, the Hungarian forest law prohibited conversion of forest to grassland. Recent legislative changes now allow for this type of conversion in protected areas where unfavourable site conditions prevail and reforestation is not feasible by using native tree species. In the region, the regeneration of dry sand grasslands can take place almost exclusively in abandoned agricultural areas and in the place of protected non-native plantations where forest-grassland conversion can be carried out. However, there are many factors that may constrain vegetation regeneration in old-fields and in former plantations such as the presence of invasive species, absence of propagules of native species, changing soil conditions, and accumulated litter on the soil surface. In my thesis, I studied the spontaneous regeneration of sand grasslands and the restoration of open sand grasslands with a focus on these constraining factors.

In the first case study, we studied the recovery potential of open (*Festucetum vaginatae*) and closed grasslands (*Galio veri-Holoschoenetum vulgaris, Pseudolysimachio spicatae-Salicetum rosmarinifoliae)* in burnt pine plantations over five years following the pine removal through burning in the Késeshalmi Sand Dunes Protected Area. We compared soil characteristics and vegetation composition in recovering and control (natural) grasslands at two elevation zones. My specific questions were the following: Does the soil of recovering stands differ from that of neighbouring natural grasslands? Does the recovering vegetation differ from neighbouring natural grasslands in species richness and composition? Do differences between low and high elevation natural grasslands re-emerge between the low and high elevation recovering stands?

In the second case study, we tested experimentally three major factors that may constrain the restoration of open sand grasslands in former pine plantations following burning in the study area of the first case study. My specific questions were the following: Does the removal of pine litter facilitate grassland recovery? Does the seeding of native grasses (*Festuca vaginata* and *Stipa borysthenica*) enhance the regeneration of open sand grasslands? Does the presence of *Asclepias* affect the regeneration of grassland vegetation?

In the third case study, we experimentally manipulated the abundance of the invasive common milkweed to assess its impact on vegetation recovery in an invaded old-field neighbouring the strictly protected Fülöpháza Sand Dune Area. We eliminated the aboveground cover of milkweed for 2 years with repeated mechanical shoot removal and assessed whether milkweed affected the germination and establishment of two dominant grass species of open sand grasslands during secondary succession. My specific question was the following: Does the presence of milkweed shoots affect the germination rate and the survival of sown grasses in two years with contrasting weather conditions?

MATERIAL AND METHODS

SPONTANEOUS REGENERATION OF OPEN SAND GRASSLANDS IN BURNT PINE PLANTATIONS

The study site of the first and second case studies was a 60 ha unit in the Kéleshalom Sand Dune Area. The dominant soil type is Calcaric Arenosol (calcareous sand soil with sand content over 90% and humus content below 1%). The site is a sand dune area with altitude ranging between 140-148 m a.s.l. A preliminary survey of ours found that open perennial grasslands cover sand dunes above 142 m at the study site (high zone), while closed grasslands are located in inter-dune depressions below 142 m (low zone), the latter linked strongly to historical water table levels. Pine plantations (mostly *Pinus nigra* with some *P. sylvestris*) had covered the site since the 1960-70's until 2007 when the whole area except for some small fragments was burnt in a wildfire and the pine trees were killed. The trees were removed by the end of 2008 and the area was left to spontaneous regeneration of the vegetation.

We used natural open and closed grassland patches among and around burnt pine stands as control and compared them to the recovering stands. We established ten permanent 4 m x 4 m plots in each of five habitat categories: low-zone and high-zone recovering grasslands, low-zone and high-zone control grasslands and high zone unburnt pine plantations.

In 2009, soil samples were collected within each recovering and control plot. Soil samples were analysed for texture, pH, humus content, AL-soluble available phosphorus, AL-soluble potassium, available nitrate and ammonium, and $CaCO_3$ content. Vegetation plots were monitored by visual cover estimation of vascular plant species in July and October each year between 2008 and 2012. Summer and autumn data were merged by using maximum cover value for each species within each year.

Linear models were used to investigate the differences in soil parameters in the recovering and control plots at the two elevation zones two years after the fire. Linear models, generalized least squares and general linear models were applied to show significant differences in total species richness, total cover, species richness and cover of species characteristic to open and closed grasslands, and exotic species five years following the fire. Multivariate methods (non-metric multidimensional scaling, multiple response permutation procedure) were implemented to assess grassland recovery by using presence-absence data of unburnt pine plantation at the start of the sampling period (in 2008) and recovering and control grasslands at the end of the sampling period (in 2012). We performed indicator value analysis to find species indicative of each habitat category. We used Spearman rank correlation to examine if the five-year average cover of two dominant species of recovering grasslands (the exotic *Asclepias syriaca* and the native *Calamagrostis epigeios*) was correlated with the species richness and cover of natural grassland species in 2012. *Calamagrostis* was not treated as a part of the natural grassland species group. All calculations in the three case studies were performed in the R statistical environment (R Development Core Team 2012).

RESTORATION OF OPEN SAND GRASSLANDS IN BURNT PINE PLANTATION

In 2008, 20 treatment blocks of 3 x 3 m were established in the Késleshalom study site. Ten blocks were placed in stands that were invaded by common milkweed and ten were placed in stands free of milkweed invasion. Blocks were placed in dune tops and sides above 142 m a.s.l. as our focus was on open sand grasslands. Each block consisted of four 1 m x 1 m plots with the following treatments: seeding, litter removal, seeding plus litter removal, and untreated control. In autumn 2008, litter was removed with a hand rake in litter removal and in seeding plus litter removal plots. In seeded plots, a mixture of *Festuca* (1 g/m^2) and *Stipa* (1.3 g/m^2) was seeded.

The percentage cover of vascular species was visually estimated every year in June between 2008 and 2014, and the seedling number of seeded grasses was counted in 2009. In 2014, ten reference grassland plots of 1 m x 1 m were selected within the study site to gather reference vegetation data in each stand. The effect of seeding, litter removal, invasion (i.e. the presence of milkweed) and year were assessed on the following response variables: seedling number and cover of *Festuca* and *Stipa*, and species richness and cover of unseeded target species. Seedling number of the two seeded species was evaluated based on the data from 2009. The other response variables were assessed throughout the study period. Linear mixed effects models and generalised linear mixed effects models were applied to investigate the differences in response variables among treatments. We applied Non-metric Multidimensional Scaling to visualize the temporal shifts in vegetation composition by plotting treatment plot averages between 2008 and 2014 and the average of reference grassland plots in 2014.

RESTORATION OF OPEN SAND GRASSLANDS IN OLD-FIELDS INVADED BY COMMON MILKWEED

The study was conducted in an abandoned field of 22 hectares neighbouring the strictly protected Fülöpháza Sand Dune Area. The 22 hectares site was covered by open sand grasslands until the 1950's. It was used as a vineyard between the 1960's and 1980's. The area was transformed to grey poplar (*Populus* x *canescens*) plantation in 1989 but poplar trees failed to establish due to wood theft on the largest part of the site. Subsequent spontaneous regeneration resulted in a vegetation similar to old-fields in the surroundings with large treeless grassland patches interspersed with some grey poplar tree groups. According to aerial photographs, the site has been invaded by *Ascepias* by 2000.

In a 10 ha treeless area of the abandoned field, we selected altogether 36 2x2 m plots invaded by *Asclepias* in September 2010. We designated the plots where *Festuca vaginata* and *Stipa borysthenica* did not occur, and the total cover of perennial plant species did not exceed 10%. The mean shoot number of *Asclepias* was 45.8 per plot (+/- 11,5 SD). *Tortula ruralis*, a moss species dominant in abandoned fields, covered the plots with an average cover of 95%. Therefore, as a pre-treatment, we removed the moss layer with a rake from each plot to help seed germination. We intended to assess the effect of milkweed shoot removal therefore, half of the plots were cleared from milkweed shoots by regular hand pulling (six times per year between September 2010 and September 2012). In September 2010, we seeded two native grass species *Festuca* and *Stipa* in twelve plots each (third of the plots were left unseeded). This resulted in six treatment combinations with six repetitions.

The number of milkweed shoots and number and cover of the two grass seedlings were assessed for two growing seasons. Linear mixed effects models and generalized linear mixed effects models were applied to investigate the differences in the response variables among the treatments.

NEW SCIENTIFIC RESULTS

SPONTANEOUS REGENERATION OF OPEN SAND GRASSLANDS IN BURNT PINE PLANTATIONS

(1) Soil characteristics in former burnt pine plantations did not limit spontaneous regeneration of sand grasslands.

We found only minor soil differences between recovering and control stands. In both elevation zones, we found lower silt and humus and higher phosphorus content in the recovering plots than in the controls. The other assessed soil characteristics did not differ between recovering and control grasslands. We argue that the observed differences in soil parameters are relatively small, and the soil remained extremely coarse-textured and nutrient poor similar to that of the reference grasslands, which implies that altered abiotic conditions are unlikely to pose a major limitation on vegetation recovery.

(2) Five years following the fire the spontaneous regeneration of the vegetation was partial in the place of the burnt pine plantations.

The total species richness and species cover did not differ in recovering and control grasslands. Open sand grassland species, which dominated high-zone control grasslands, recovered in both zones in terms of species richness, but not in cover. Closed grassland species, which dominated low-zone control grasslands, did not recover in terms of either species richness or cover except for a single native weed *Calamagrostis epigeios*, typical to natural closed grasslands. Both open and closed control grasslands had mostly perennial indicator species characteristic regionally to open and closed sand grasslands. The indicator species of recovering grasslands were mostly annual weed species. In the recovering grasslands in the high zone, *Asclepias* was the single dominant indicator species, while in low-zone recovering stands, *Calamagrostis* and *Asclepias* dominated the vegetation.

(3) The high regeneration of open sand grasslands and the limited recovery of closed grasslands together with the zone-independent spread of common milkweed led to biotic homogenization in the former burnt plantations.

Species of open sand grasslands established in both low and high zones, while closed grassland species did not appear except for *Calamagrostis* in neither zones. Recovery went in the direction of open sand grassland vegetation in both zones in terms of species composition. Common milkweed was already present in the 70 % of the recovering plots in both zones in 2012.

(4) We did not find any correlation between milkweed cover and the abundance of natural grassland species. Similarly, we could not detect any correlation between *Calamagrostis* cover and the abundance of natural grassland species.

We did not find any correlation between milkweed cover (average of 2008-2012) and either the species richness or the cover of natural grassland species in 2012 according to Spearman rank correlation. Similarly, *Calamagrostis* cover was not significantly correlated to either the species richness or the cover of natural grassland species in 2012.

RESTORATION OF OPEN SAND GRASSLANDS IN BURNT PINE PLANTATION

(5) Secondary pine litter that fell on the soil surface following the burning of original pine litter and tree burning did not limit regeneration of open sand grassland.

Litter removal reduced seedling number of *Festuca* by almost 20 % compared to that in plots without litter removal in the first year after seeding, but this difference had disappeared by the seventh year after seeding. Litter removal had no effect on the seedling number and cover of *Stipa*. Neither the richness nor the cover of unseeded target species were affected by pine litter removal.

(6) Seed sowing of the two dominant grass species (*Festuca and Stipa*) helped to recover quickly the main matrix of the grassland but the high seeding density limited the spontaneous establishment of unseeded species characteristic to open sand grasslands.

Seeding of *Festuca* and *Stipa* had an overwhelming effect on vegetation development. Seed addition enhanced the regeneration of open sand grassland in terms of the abundance of seeded species suggesting low propagule availability of native grasses despite the presence of propagule sources within and around the study site. As an adverse side effect of seeding, seeded grasses negatively affected the establishment of unseeded target species in terms of both richness and cover by reducing space available for establishment.

(7) Invasive common milkweed did not limit native plant species in recovering open sand grassland in the place of burnt pine plantations in the first seven years of the regeneration but had some positive effect on species composition.

The presence of common milkweed did not have any major effect on the establishment of the dominant grasses. We observed a transient positive effect of *Asclepias* on *Stipa* cover and a transient negative effect on *Festuca* cover. The presence of *Asclepias* caused a small but significant increase in the richness of unseeded target species, while it had no effect on the cover of these species.

RESTORATION OF OPEN SAND GRASSLANDS IN OLD-FIELDS INVADED BY COMMON MILKWEED

(8) The presence of invasive common milkweed did not reduce germination and early establishment of *Stipa* and *Festuca* in recovering old-field vegetation. During the summer drought in the second year, the number and cover *Festuca* individuals were higher in plots covered with *Asclepias*, while Stipa abundance was not affected significantly by *Asclepias*.

We did not find any effects of *Asclepias* on the number and cover of *Festuca* seedlings in 2011. Nevertheless, this neutral effect turned into positive during the summer drought in 2012, when both the number and cover of *Festuca* seedlings became significantly lower in plots where *Asclepias* shoots were removed. Shade provided by the foliage and litter of *Asclepias* seemed to mitigate unfavourable abiotic conditions for *Festuca* caused by summer drought. We did not observe any impact of *Asclepias* shoots in case of *Stipa* in either year. The differential effect of *Asclepias* for the two seeded grasses may be the result of their differential drought tolerances.

CONCLUSIONS AND PROPOSALS

Despite the presence of several land use legacies, we conclude that sand grasslands have a high restoration potential in burnt pine plantations when propagules of native species are available. Open sand grasslands have high regeneration potential as they are independent of the water table level and have larger natural fragments left within the region. Closed sand grasslands could not recover spontaneously in either of the zones probably because of propagule limitation and adverse abiotic conditions. The latter is most likely due to a regional decline in soil water table thus a local restoration measure may have limited effect on recovery and the disappearance of closed grasslands is irreversible with only local activities. Conservation efforts here should focus on the preservation of primary closed grasslands in order to maintain a landscape-scale mosaic of open and closed grasslands.

The minor soil differences we found between recovering and control stands of former burnt pine plantations suggest that altered abiotic conditions are unlikely to pose a major limitation on vegetation recovery. We also showed that secondary pine litter removal does not help open sand grassland recovery in former burnt pine plantations. This implies that restoration measures do not need to bother with soil remediation. Indeed, the high number of grassland species present shortly after the start of secondary succession indicates that soil restoration measures that may potentially limit species colonisation, such as trunk removal and ploughing, should be avoided.

Species characteristic to open grasslands established in many spontaneously recovering grasslands plots, but their cover was extremely low in the former burnt pine plantations. Our findings underlined the importance of seed addition as an effective management option against propagule limitation that accelerates the recovery of the grassland matrix within a relatively short time. However, the applied seeding density of grasses (2.3 g m^{-1}) influenced the abundance of unseeded open grassland species. Therefore, if the goal is to restore vegetation composition, lower seeding density of grasses should be applied.

We found no evidence that the presence of *Asclepias* would negatively influence either spontaneous or assisted grassland recovery in former burnt pine plantations and old-fields, which implies that its removal may not be necessary to reach biodiversity targets in these nutrient-poor water-limited ecosystems. We even detected some positive effects on the species composition in former pine plantations and on *Festuca* survival in the old-field during summer drought. However, further information is needed about milkweed effects in later phases of secondary succession and on other elements of the biota. Our *Asclepias* shoot removal treatment mimicked mowing, which is a frequently used control method against the species. We showed that mechanical shoot removal is an ineffective way of eradication. In fact, attempts to control *Asclepias* (e.g. by spraying or mechanical control) may compromise biodiversity. The eradication of milkweed in sandy habitats is controversial with high financial costs, low long-term efficacy, serious non-target effects, and possible soil disturbance that help *Asclepias* re-establishment from its abundant soil seed bank. Therefore, the evaluation of ecological and economic costs and benefits of *Asclepias* control should be carefully implemented so that the present and potential future impacts of invasion exceed the cost of eradication.

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